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Distribution modelling and multi-scale landscape connectivity highlight important areas for the conservation of savannah elephants

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A R T I C L E I N F O

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A B S T R A C T

Habitat connectivity is the milestone towards species' long-term persistence, especially considering impacts of climate change and human activities. Here, we examined the potential implications of climate change and human pressure on connectivity among habitat patches, aiming to identify priority areas and potential corridors for elephant conservation. We used an ensemble modelling approach to evaluate the potential climatic distribution of the savannah elephants *Loxodonta africana* through time. We considered different climatic scenarios and used current potential climatic suitability and human pressure to evaluate habitat quality for the species. In addition, we used habitat quality and the centroids of elephant patches to evaluate habitat connectivity considering four progressive dispersal distances (100 km, 200 km, 300 km, 400 km). Elephant response to climate change has been conservative through time with overall slight improvement in climatic suitability in southern and eastern Africa and reduction in western Africa and northern portions of central Africa. Habitat quality followed the distribution of currently suitable areas for the species. We found three major areas with high density of least-cost paths in southern, eastern and western Africa, identifying them as potential areas for increasing the connectivity of elephant populations.

1. Introduction

Global climate change is shifting biodiversity patterns (Wan et al., 2014; Yannic et al., 2013) and current reports show that its effect on biodiversity will likely increase in the near future (de Oliveira et al., 2012; Hoglund, 2009). This large inferred increase in effects, has motivated multiple efforts to better understand these implications on different taxa and species and safeguard their survival and long-term persistence. However, the effect of climate change on biodiversity patterns is still an open field given the uncertainties associated with existing data (Garcia et al., 2014; Loyola et al., 2012).

Among several approaches applied to understand the implications of climate change on species, species distribution modelling (SDM) has been identified as a useful tool to understand how species will respond to changing climates (Pacifici et al., 2015). These models put emphasis on the combination of data on species observations and environmental variables to model past occurrences and identify areas with appropriate climate conditions for the species (Brown and Yoder, 2015; Summers et al., 2012). This is especially important for species with large and discontinuous ranges, such as African elephants. Nevertheless, climate change is not the single threat to biodiversity and other approaches are needed to revert current rates of biodiversity extinctions (Johnson et al., 2017; Avise et al., 2008).

Apart from modelling the potential distribution of species under changing climate scenarios, other approaches are being implemented, integrating not only climate change but also the impact of other drivers of biodiversity change such as land use and habitat fragmentation and isolation (Zwiener et al., 2017; Mazziotta et al., 2015). Thus, the urgency for identifying suitable habitats that can, at the same time, accommodate the impacts of changing climates and the impacts of other human threats, have probed the rise of landscape connectivity studies based on species requirements and landscape quality (Rattis et al., 2018), to identify sites that if protected can ensure easy species dispersal (Keeley et al., 2017; Rubio et al., 2015). Most of these approaches have been developed to assess landscape connectivity based on graph theory (Almasieh et al., 2016; Balkenhol et al., 2015), focusing on least-cost models (Adriaensen et al., 2003), circuit theory (Mcrae et al., 2008) and centrality analyses (Estrada and Bodin, 2008).

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Savannah elephants currently have their habitat distributed across 18 countries (Chase et al., 2016). Recent estimates from the Great Elephant Census (GEC) revealed extensive population declines with some populations in Tanzania, Mozambique, Angola, Cameroon and Zimbabwe having a declining rate of > 5%/year, mostly associated with poaching (Chase et al., 2016; Wasser et al., 2015). Previous studies have indicated that despite the fact that African elephants are a widespread species living across diverse habitats with numerous food sources, they are vulnerable to climate change as a result of their sensitivity to high temperatures, susceptibility to diseases, long generation length and low genetic variation (Martínez-Freiría et al., 2016; Advani, 2014).

In addition to these threats, elephants are affected by their limited dispersal among habitat spots. Because they require large areas to move, habitat fragmentation can reduce their dispersal ability, resulting in extensive impacts on the species and the ecosystems they use. As suggested, habitat fragmentation in addition to preventing the movement of elephants leads to the confinement of elephants in small areas, resulting in deleterious effects (Estes et al., 2012; Cushman et al., 2010). As a consequence, high elephant population density in some regions result in degradation of vegetation and reduced elephant ability to respond to changes in the landscape and in climate (Estes et al., 2012), jeopardizing the species (Blake et al., 2008). Although some degree of range reduction is expected as a result of climate change (Martínez-Freiría et al., 2016), no extensive study has been done to simultaneously understand how historical climate change has shaped *L. africana* distribution, the evolution of elephants' climatic niche and proposed potential areas to be safeguarded to enable habitat connectivity across the entire range of the species.

Considering the above mentioned threats, the identification of priority areas for landscape connectivity incorporating climate change and habitat quality for savannah elephants can be instrumental to rescue existing habitats, ensure their connectivity and safeguard remaining populations (Balkenhol et al., 2015; Guan et al., 2016). Here, based on occurrence records of the African savannah elephant, high-resolution climate data and the centroids of sites with known elephant presences, we modelled the distribution of the species aiming to inform past, present and future responses and the geographic shifts in suitable areas for the species. Then, we evaluated whether the environmental space of savannah elephants had evolved following different climatic times by measuring pairwise niche overlap, estimated priority areas for the establishment of habitat connectivity corridors and assessed the degree of overlap between potential corridors and the current network of protected areas. Specifically, we answer the following question: considering the combined impacts of climate change and human pressure, which are the most important areas for increasing connectivity among savannah elephant populations?

2. Material and methods

2.1. Conceptual framework

In this study, we combined two broad approaches that have been largely applied in biodiversity conservation to mitigate the combined effects of climate change and human disturbance. First, we used species distribution modelling to understand potential implications of climate change on savannah elephant range shifts based on a combination of publicly available species occurrence records and environmental variables. Then, we combined current climatic suitability and the human footprint index to develop an index of habitat quality. The habitat quality index was then used to calculate the probability of landscape connectivity between sites with confirmed savannah elephants, in order to prioritize areas for conservation (Fig. 1).

2.2. Species occurrence records and environmental variables

We obtained elephant occurrence records from publicly available databases (Global Biodiversity Information Facility (GBIF, www.gbif.org) and online reports (AGRECO, 2008). We also incorporated a set of occurrence records previously published elsewhere (Martínez-Freiría et al., 2016). Our final dataset comprised 2774 independent occurrence records (see Table S1), from which 24 were fossil data retrieved from the PaleoBiology database (https://paleobiodb.org). We obtained 19 climate variables from the World Climate Database (WorldClim, http://www.worldclim.org, Hijmans et al., 2005) at a spatial resolution of 10 arc-min (ca. 18 km at the equator) representing Last Glacial Maximum (LGM), Mid-Holocene (MidH), Current and Future climate scenarios. For the Last Interglacial (~120–140 ka, LIG) we downloaded data at a resolution of 30 s and then interpolated to the resolution of other time slices using the SDMToolbox v1.0 (Brown, 2014) in ArcGIS 10.5. For future scenarios, we downloaded data of four representative concentration pathways (RCP 2.6, 4.5, 6.0 and 8.5) for 2050 and 2070 (van Vuuren et al., 2011), derived from CCSM4 and MIROC-ESM Ocean-Atmosphere Global Circulation Models (AOGCMs).

2.3. Past, present and future species distribution modelling

We modelled the potential distribution of savannah elephants using ten modelling algorithms (Generalized Linear Models – GLM; Boosted Regression Trees – GBM; Generalized Additive Model – GAM; Classification Tree Analysis – CTA; Artificial Neural Network – ANN; Surface Range Envelop or BIOCLIM – SRE; Flexible Discriminant Analysis – FDA; Multiple Adaptive Regression Splines – MARS; Random Forests – RF) available in the *biomod2* package (Thuiller et al., 2016) in R (R Core Team, 2017) and the stand-alone maximum entropy algorithm (MaxEnt v3.4.1; Phillips et al., 2006). Models were created by subsampling occurrence data into 75% for training and 25% for testing (Phillips et al., 2006; Sobek-Swant et al., 2012).

Considering that species distribution models are not explicitly spatial and that climate variables might be influenced by similar patterns, thus being non-independent (Franklin, 2010), prior to modelling we undertook a variable selection through principal components analysis (PCA) to reduce redundancy and autocorrelation. These analyses were done using the PCA toolbox in ArcGIS and the resulting three components (Fig. S1), explaining 99% of the total variance, were used for modelling the distribution of savannah elephants, largely related to temperature and precipitation variations (Janžekovič and Novak, 2012).

Following other studies, we considered the African continent as the study area, excluding all island countries/territories (Barnes, 1999; Martínez-Freiría et al., 2016). We modelled the potential current distribution of the species and then projected the model into past and future climate scenarios. For each climate scenario, we obtained consensus maps following an ensemble approach in which all maps were averaged based on the average AUC value (Lima-Ribeiro et al., 2017; Alabia et al., 2016;). We evaluated models' predictive ability by their respective area under the curve of the receiver operating characteristics (AUC) and the “true skills statistics” (TSS).

2.4. Spatial analysis of range dynamics through time

To understand the spatial dynamics of the environmental niches through time we used a two-fold approach. The first approach was based on the outputs generated by the modelling algorithms. Based on the continuous maps we quantified the pairwise pixel-based change in climatic suitability, thus identifying areas which increased or reduced suitability. Then, we applied the specificity-sensitivity threshold and converted all continuous maps into binary distributions that were used to calculate range size and range gains and losses, the same approach applied elsewhere (Lima-Ribeiro et al., 2017; Saupe et al., 2015).

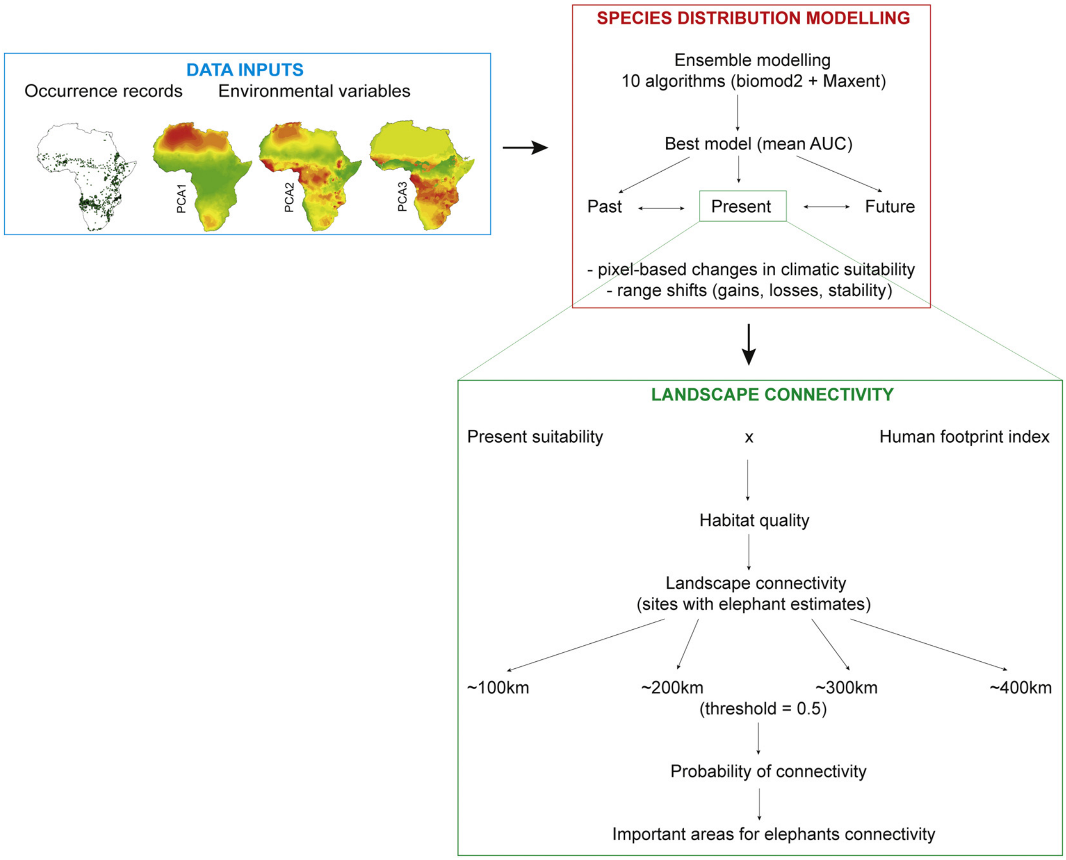

Fig. 1. Summary of the methodological approach applied in this study.

Analyses were done in R (R Core Development Team, 2016) and ArcGIS 10.5.

The second approach was based on the physiology of savannah elephants. One of the features characterizing African elephants are their ability to cope with a wide range of habitats and environmental conditions, as exemplified by the presence of elephants in desert and semi-arid places (e.g. desert elephants of Namibia and northern Mali), in high altitude (e.g. mount Kilimanjaro) and extensive plains. In addition, representations of historical range of African elephants describe elephants as occupying most of the African continent. As such, we wanted to test whether elephants exhibit greater adaptability or whether the currently occupied range has similar climatic conditions as in the past, mostly because distributional shifts may create spatial variations in similarities between two time slices. For this, we used the continuous distribution to evaluate pairwise niche similarities or differences in the environmental space based on the Schoener's *D* (*D*) and *I* statistic (*I*), both ranging from 0 (niches completely different) to 1 (niches overlapping) (Broennimann et al., 2012). We did these analyses using the *nicheOverlap* function of the *dismo* package (Hijmans et al., 2017) in R (R Core Team, 2017).

2.5. Delineating priority landscapes for conservation

A great priority in ensuring species persistence is the identification of suitable pathways that can connect populations across the landscape (Carvalho et al., 2016; Xun and Liu, 2014). Considering that the current rate of habitat loss might impair species connectivity and persistence, we identified priority conservation landscapes for savannah elephants using Conefor Sensinode 2.2 (CS22; www.conefor.org; Saura and Torné, 2009) and ArcGIS 10.5. This analysis requires a landscape resistance layer and unique sampling localities to create least-cost corridors and least-cost paths between habitats (Fan et al., 2017; Brown, 2014). We combined raster maps of current suitability with the inverted human footprint index (HFP; Sanderson et al., 2002) to generate a continent-wide index of habitat quality and used this as a landscape resistance layer to input in ArcGIS in association with the habitats with confirmed elephant numbers, as provided by the 2016 African Elephant Status Report (AESR; Thouless et al., 2016).

Following approaches applied elsewhere (Xun and Liu, 2014; Carvalho et al., 2016), we generated population connectivity maps by summing pairwise least-cost paths (LCPs) between habitat centroids to create cost distance using the Conefor Inputs toolbox (http://www.jennessent.com/arcgis/conefor_inputs.htm) in ArcGIS 10.5. Then, we measured habitat availability based on the probability of connectivity (PC) between nodes and habitats, calculated for four progressive dispersal scenarios of 100 km, 200 km, 300 km and 400 km, with the probability threshold set at 0.5. Probability of connectivity is the probability that two animals randomly placed in a landscape fall into interconnected habitats, given a number of habitat patches and the connections among them (Saura and Pascual-Hortal, 2007), considering habitat loss and functional connectivity (Saura et al., 2011). Probability of connectivity is calculated as

$$\mathrm{PC} = \frac{\sum_{i=j}^{n}\sum_{j}^{n} \mathrm{a_i}.\ \mathrm{a_j}.\ \mathrm{p}_{ij}^{*}}{\mathrm{A}_L^2} \tag{1}$$

where, a_i and a_j represent the patches between sites *i* an *j*, $A_L{}^2$ is the total landscape area and $p_{ij}{}^*$ is the product of all p_{ij} values for all connections in habitat patches. PC ranges from 0 to 1 with values near 1 showing high connectivity (Saura and Pascual-Hortal, 2007).

Further details on the calculations of this index are extensively described elsewhere (Xun and Liu, 2014; Saura et al., 2011; Saura and Pascual-Hortal, 2007; Saura and Torné, 2009; Liu et al., 2014). We chose PC among several other indexes because it is not affected by the presence of adjacent habitat patches or cells (Pereira et al., 2017; Saura

and Pascual-Hortal, 2007). Based on this index, CS22 enables the calculation of the local node importance index (dPC) that ranks habitat patches as an order of importance for connectivity in the landscape by quantifying the effect of the removal of nodes (or group of nodes) on the overall connectivity of the network (Pereira et al., 2017; Saura and Rubio, 2010). The number of elephants and habitat quality were used to normalize dPC values for each habitat patch. Considering the urgent need of securing currently connecting available habitats, we only modelled landscape connectivity (PC and dPC) for the present scenario.

2.6. Additional statistical analysis

We used the above information on current habitat quality (climatic suitability + human footprint index) to test whether protected areas (PAs) harbour areas with highest quality for savannah elephants. We used the database of global PAs from the World Database on Protected Areas (http://www.protectedplanet.net) and extracted all PAs located in Africa. We generated 1000 spatially balanced points using the Sampling Network Design of the Geostatistical Analyst Toolbox in ArcGIS 10.5 and each point was assigned a value of "1" if it falls within the boundaries of a PA and a value of "0" if it falls outside a PA. We used *t*-test within grids to compare current habitat quality between within and outside PAs, the same approach applied elsewhere (Caten et al., 2017). We, then, applied a paired *t*-test to check whether there were differences in dPC between elephant habitats (Thouless et al., 2016) with increasing dispersal distance (100 to 400 km), but maintaining the same probability threshold of 50%.

3. Results

Overall, niche models had reliable predictive performance (Table S2) with all TSS above 0.5 and AUC values above 0.8. These predictions indicated niche dynamics through time with the present potential distribution approximating the area of occupancy (AOO) generated by the International Union for Nature Conservancy (IUCN) and the African Elephants Database (AED) (Fig. 2d). Past distributions showed suitable areas for savannah elephants at the Eastern and Southern Africa (Fig. 2a–c) with an increase towards the southern border of the Sahara Desert and through Western Africa during the Last Glacial Maximum (Fig. 2b) and Mid-Holocene (Fig. 2c). This trend, however, proved to be a stable environment for future scenarios, with an increase in suitability at the southern border of the Sahelian region and the eastern and southern regions (Fig. 2e–f). Our results showed a continuous reduction of suitable habitats in central Africa that might be completely lost by 2070 (Fig. 2f).

Overall, the dynamics of the climatic range of savannah elephants had pairwise increases and decreases in habitat suitability, as indicated in Fig. 3. For example, between the LIG and the LGM, there was an extensive increase in suitable habitat (Fig. 3a) that was nearly completely lost during the following pair of climate scenarios (Fig. 3b) and regained during the transition between the Mid-Holocene and current climatic conditions (Fig. 3c). For future scenarios, relatively few

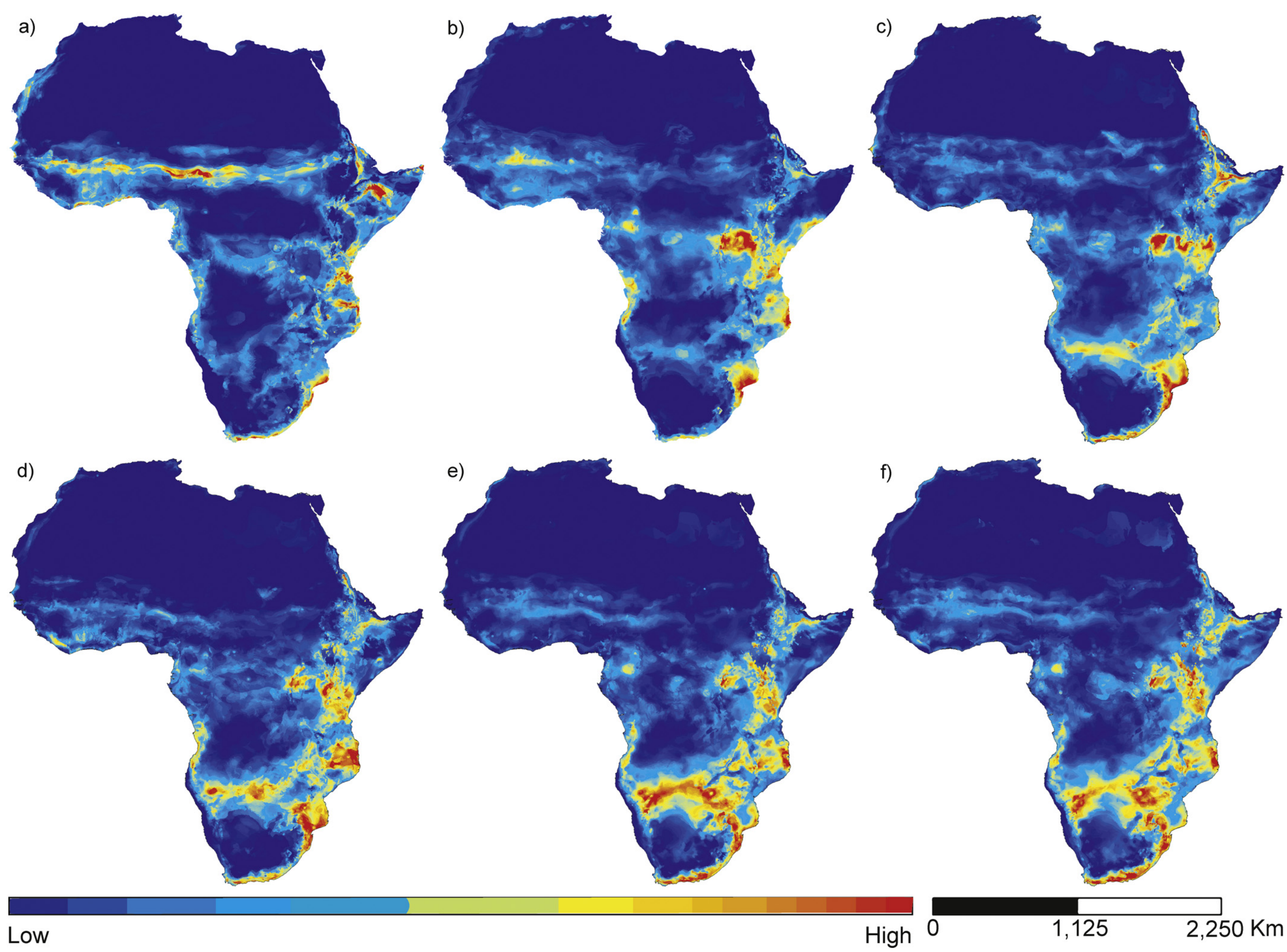

Fig. 2. Potential climatic suitability for savannah elephants through time, measured as a consensus (average) between 10 modelling algorithms. a) Last Inter-Glacial (~120 kya–140 kya), b) Last Glacial Maximum (~21 kya), c) Mid-Holocene (~6 kya), d) Present (1960–1990), e) Future (2050), f) Future (2070).

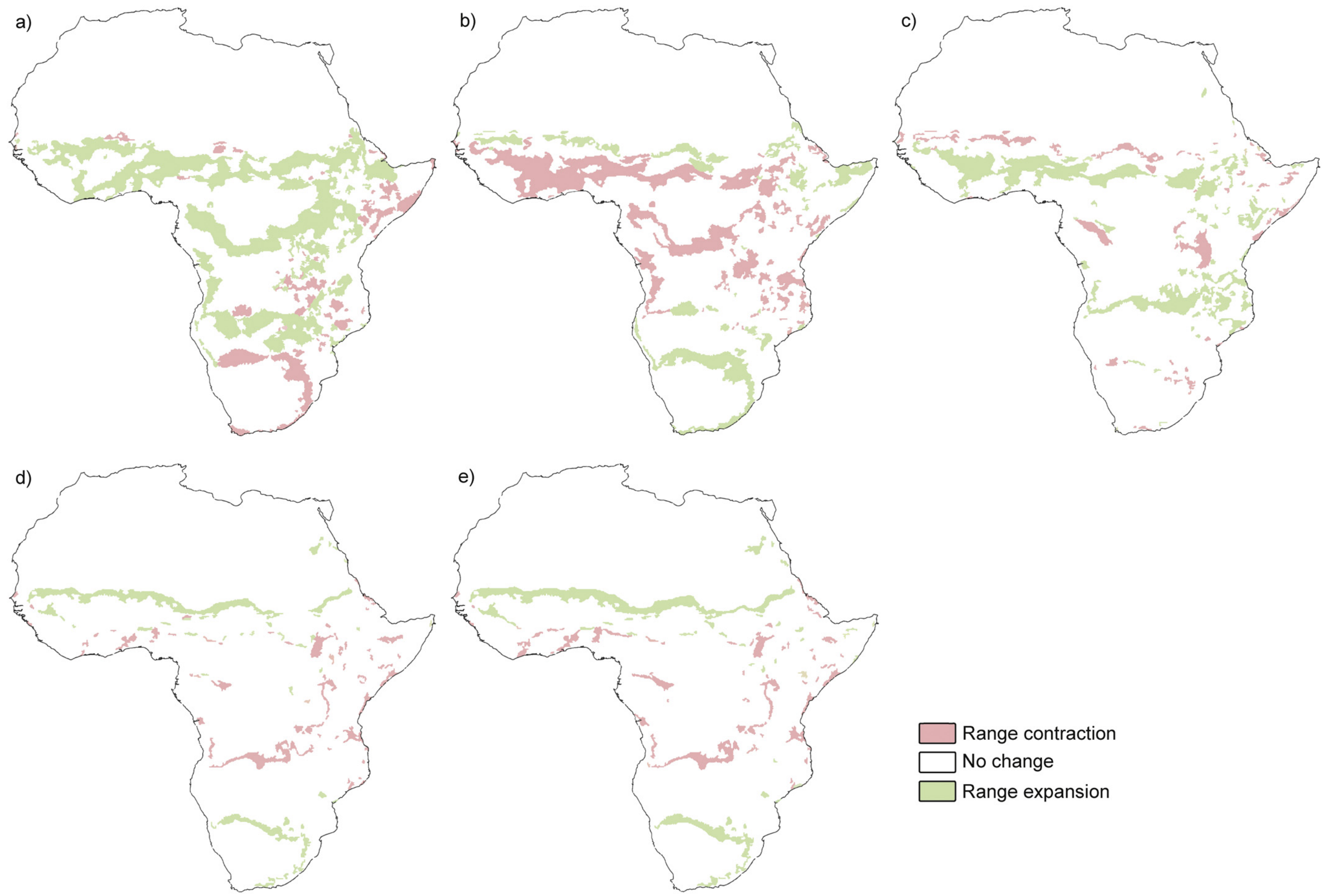

Fig. 3. Loss and gains in habitat suitability through time. Range shifts between a) LIG–LGM, b) LGM–Mid-H, c) Mid-H–Present, d) Present–Future (2050), e) Present–Future (2070).

Table 1
Pairwise niche gains, losses and overlap (measured using Schoener's *D* and Hellinger's *I* statistics) through time. Columns a) and b) represent the percentage of savannah elephants suitable area that were (or will be) potentially gained or lost across two consecutive climatic scenarios (beginning (time A) and end (time B)) and columns c) and d) represent the probability of similarity between climatic conditions in suitable areas, across two consecutive climatic scenarios. LIG stands for "Last Interglacial" (~120 kya–140 kya), LGM stands for "Last Glacial Maximum" (~22 kya), MidH stands for Mid-Holocene (~6 kya). Present corresponds to the current environmental conditions (1960–1990) and 2050 and 2070 correspond to the projected environmental condition of (2041–2060, 2061–2080) averaged considering four RCPs and two AOGCMs (CCSM4 and MIROC-ESM).

Time A	Time B	a) Gains	b) Losses	c) Schoener's *D*	d) Hellinger's *I*
LIG	LGM	17.346	4.385	0.478	0.599
LGM	MidH	5.853	10.862	0.662	0.746
MidH	Present	8.98	3.033	0.736	0.832
Present	2050	3.901	2.992	0.850	0.921
2050	2070	1.551	0.795	0.955	0.979
Present	2070	4.938	3.273	0.824	0.904

changes in habitat suitability would be expected (Fig. 3d–e, Table 1). Comparatively, the transition between the LIG and LGM experienced the highest gains in suitable climatic habitat, while the transition from the LGM to Mid-H experienced the highest loss of climatically habitat (Table 1). These transitions did not, however, imply strong niche evolution. As shown in Table 1, climatic conditions in different scenarios tended to be equivalent, with both *D* and *I* statistics indicating high climatic overlaps between time slices.

Habitat quality followed the distribution of climatically suitable areas for savannah elephants (Fig. S2). This result indicates that potential conservation areas are those that have high climatic suitability and are not, yet, heavily affected by human presence. Areas within PAs had higher habitat quality (mean = 0.53, SD = 0.13) than areas outside (mean = 0.62, SD = 0.14; $t(167.2) = -6.9$, $p < 0.001$), suggesting that African PAs are pristine habitat for savannah elephants and their enforcement is thus mandatory to ensure habitat connectivity and species persistence.

Overall, habitat patches had average probability of connectivity at all distance threshold (Fig. 4, Table 2, Table S3). At any of the considered dispersal distances, habitat patches in southern Africa had the highest connectivity importance, followed by those located in eastern Africa (Fig. 4a–d), reinforcing the importance of southern and eastern habitat as important areas for the survival of the species. Habitat importance (dPC) between elephant patches varied from 0.34 ± 0.26 (dispersal distance = 100 km) to 0.46 ± 0.27 (dispersal distance = 400 km). This result indicates that appropriate connectivity for elephants is not dependent on the distance between habitats, but on the possibility of reaching even further habitats. Increasing the dispersal distance did not alter habitat importance, although it seemed to increase dPC values (Fig. 4; Table S3). Regardless of the dispersal distance, top patches remained constant all over the continent, however, when we simultaneously considered habitat importance normalized by the number of elephants at each site, some patches appeared to be more important than others (Fig. 4a–d). The number of elephants within each habitat tended to reduce site importance, while habitat quality tended to increase the importance of elephant patches (Fig. 4).

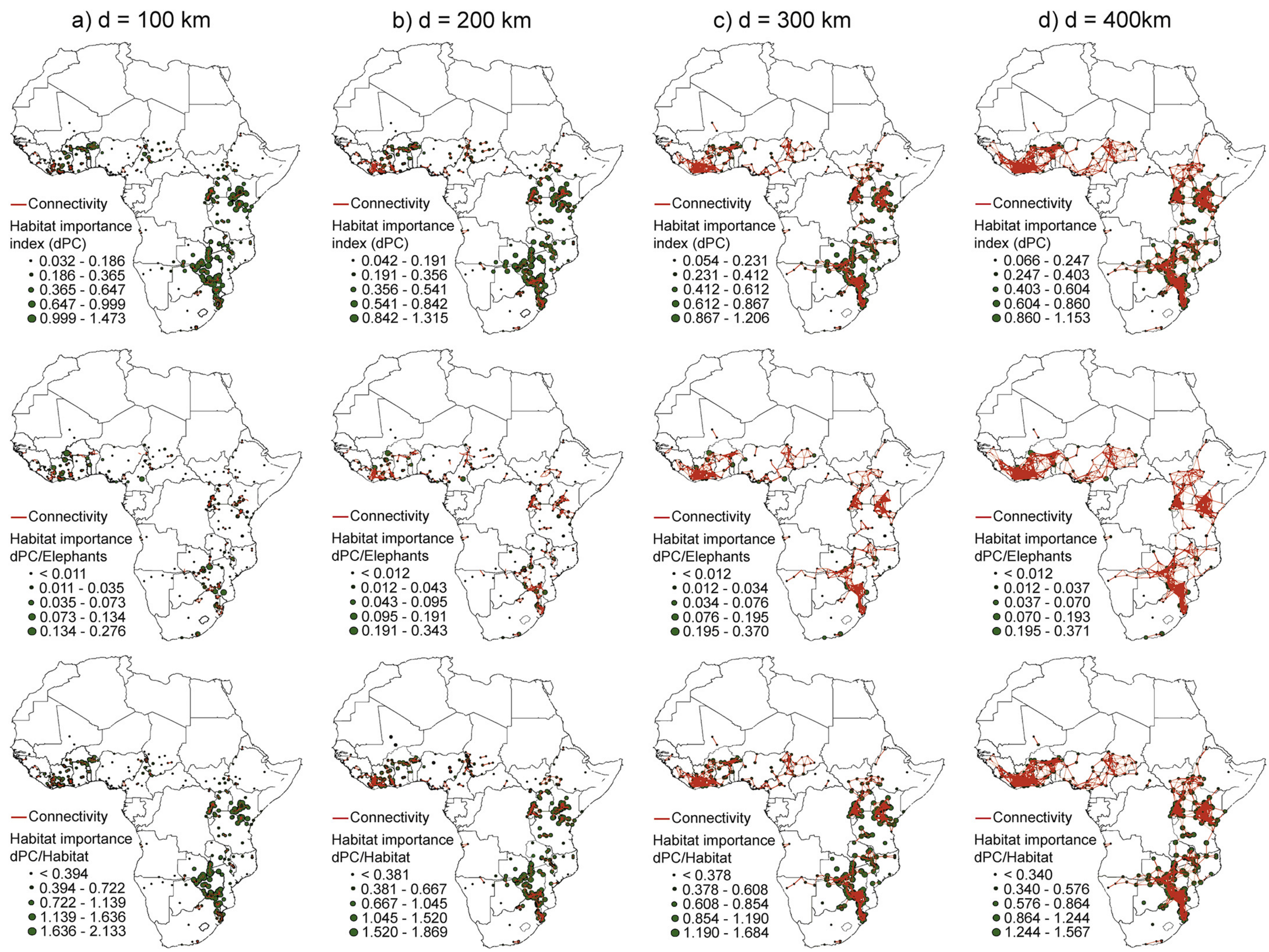

Fig. 4. Connectivity and habitat importance values at different dispersal distances. Each column (a–d) indicates values for each dispersal distance, the connectivity, habitat importance and habitat importance normalized by the number of elephants and habitat quality (measured by averaging current suitability and human footprint).

Table 2
Variation of the importance of savannah elephant patches, considering different dispersal distances.

	Dispersal distances			
	100 km	200 km	300 km	400 km
Minimum	0.032	0.042	0.054	0.066
Maximum	1.473	1.315	1.206	1.153
Mean	0.543	0.560	0.567	0.571
Standard deviation	0.412	0.375	0.345	0.324

4. Discussion

This study is the first attempt to identify potential areas for the implementation of elephant corridors throughout its entire geographic range, by combining climatic suitability from distribution modelling and human pressure. We have demonstrated that the association between climate change and habitat quality is an important aspect to be considered to ensure species long-term persistence. While climate change might have driven shifts in suitable habitats, habitat degradation might be challenging the dispersal capacity of savannah elephants, restricting them to small and isolated habitat patches.

The role of climate change is two-fold: (i) it might have driven latitudinal and altitudinal migration of climatically suitable areas in the past and (ii) might possibly drive elephant populations into hotspots of vegetation change and poaching in the near future (Gonzalez et al., 2010; Wasser et al., 2015). Suitability shifts are likely associated with temperature increases and precipitation reductions that shaped latitudinal expansion of the Sahara desert (Martínez-Freiría et al., 2016; Kröpelin et al., 2008; Yan and Petit-Maire, 1994). Although there is a great extent of habitat suitable for African elephants, its quality is very low and falls within areas prone to poaching, rising temperatures, reducing precipitation, increasing wildfires and potential vegetation changes (Gonzalez et al., 2010).

Most suitable habitats are within the current extent of occurrence of savannah elephants, which creates great opportunities for their conservation, especially in southern and eastern Africa. However, most habitats are situated around seriously impacted areas with extensive fragmentation that hampers elephant movement. When coupling this situation with the challenge associated with wildlife corridors in Africa (Caro et al., 2009), the current state of deforestation imposes challenges to the long-term survival of the species, mainly because elephants require long distances to roam (Vanleeuwé and Gautier-Hion, 2002). This is critical for accessing resources that are scarce in time and space (Graham et al., 2009), enabling elephants to respond to stochastic events and climate change, as well as the ecological integrity of the landscapes.

With increasing human dominance of the landscapes around elephant habitats, the need for dispersal could be an impediment, restricting elephant to the "islands" where they currently occur and increasing the probability of human-wildlife conflicts through crop-raiding and risks to life and livelihoods (Sukumar, 1991; Hoare, 1999). Under this paradigm, there is a need to accommodate elephants inside their habitats and ensure that their dispersal routes are maintained to allow elephant movement from one area to another. Our results indicate that there is an enormous potential for the establishment of elephant corridors. As such, reinforcing these areas for conservation and recovering the already established corridors in these areas is urgent, especially considering that elephant numbers are rapidly decreasing (Epps et al., 2013). Studies have demonstrated that elephants are focal species for connectivity planning (Epps et al., 2011), because of their need for large areas (Estes, 1991) and high sensitivity to human activities (Hoare, 2000). As such, preserving savannah elephant habitats and corridors will enable the protection of other species.

We also demonstrated that elephant dispersal potential is not dependent on the size of the habitat neither on the distance between them, but on the possibility of reaching even further habitats. This is critical for elephants and protecting large landscapes would be an effective mechanism to ensure resources availability, reduce pressure over the ecosystems and ensure that distant populations communicate from time to time. In addition, it has been established that elephants prefer to roam across heterogeneous landscapes (de Beer and van Aarde, 2008; Grainger et al., 2005). Our results reinforce this idea, as the larger the landscape protected the higher the availability of food resources for the species.

5. Conclusion

This paper addresses the ecological response of African savannah elephants considering different climate scenarios and timeframes and potential connectivity between patches to inform potential movement pathways for effective management. We found that climate change might drive the fragmentation of African savannah habitats and reduce its climatic suitability. When associated with increasing human-derived habitat fragmentation this might isolate elephant populations reducing their survival potential. Southern and Eastern Africa seems to be potential strongholds for African savannah elephants, despite the fact that these populations might have a patchy distribution in the near future. In addition, we have indicated that there is potential for the establishment of corridors that might enhance the dispersal ability of African elephants, ensuring their long-term persistence through the reduction of ecosystem carrying capacity and destruction of the habitat, improvement of gene flow and improvement of elephants' viability. We suggest that there is an urgent need to focus of the development of appropriate wildlife corridors linking potential habitats as a strategy to improve the chances of elephants to thrive and reduce the impact of elephant inside small confined habitats.

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References

Adriaensen, F., Chardon, J.P., De Blust, G., Swinnen, E., Villalba, S., Gulinck, H., Matthysen, E., 2003. The application of "least-cost" modelling as a functional landscape model. Landsc Urban Plan 64, 233–247.
Advani, N.K., 2014. WWF Wildlife and Climate Change Series: African Elephant. Washington DC.
AGRECO, 2008. National Census of Wildlife 2008 – Final Report. Maputo.
Alabia, I.D., Saitoh, S.-I., Igarashi, H., Ishikawa, Y., Usui, N., Kamachi, M., Awaji, T., Seito, M., 2016. Ensemble squid habitat model using three-dimensional ocean data. ICES J Mar Sci J du Cons 73, 1863–1874.
Almasieh, K., Kaboli, M., Beier, P., 2016. Identifying habitat cores and corridors for the Iranian black bear in Iran. Ursus 27, 18–30.
Avise, J.C., Hubbell, S.P., Ayala, F.J., 2008. In the light of evolution II: biodiversity and extinction. Proc Natl Acad Sci U S A 105 (Suppl. 1), 11453–11457.
Balkenhol, N., Cushman, S., Storfer, A., Waits, L., 2015. Landscape Genetics: Concepts, Methods, Applications. Wiley-Blackwell.
Barnes, R.F.W., 1999. Is there a future for elephants in West Africa? Mammal Rev 29, 175–200.
de Beer, Y., van Aarde, R.J., 2008. Do landscape heterogeneity and water distribution explain aspects of elephant home range in southern Africa's arid savannas? J. Arid Environ. 72, 2017–2025.
Blake, S., Deem, S.L., Strindberg, S., Maisels, F., Momont, L., Ilia, I., Douglas-Hamilton, I., Karesh, W.B., Kock, M.D., 2008. Roadless wilderness area determines forest elephant movements in the Congo basin. PLoS ONE 3 (10), e3546.
Broennimann, O., Fitzpatrick, M.C., Pearman, P.B., Petitpierre, B., Pellissier, L., Yoccoz, N.G., Thuiller, W., Fortin, M.-J., Randin, C., Zimmermann, N.E., Graham, C.H., Guisan, A., 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. Glob Ecol Biogeogr 21, 481–497.
Brown, J.L., 2014. SDMtoolbox: a python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. Methods Ecol. Evol. 5, 694–700.
Brown, J.L., Yoder, A.D., 2015. Shifting ranges and conservation challenges for lemurs in the face of climate change. Ecol Evol 5, 1131–1142.
Caro, T., Jones, T., Davenport, T.R.B., 2009. Realities of documenting wildlife corridors in tropical countries. Biol Conserv 142, 2807–2811.
Carvalho, F., Carvalho, R., Mira, A., Beja, P., 2016. Assessing landscape functional connectivity in a forest carnivore using path selection functions. Landsc Ecol 31, 1021–1036.
Caten, C. Ten, Lima-Ribeiro, M. de S., Jorge da Silva Jr., N., Moreno, A.K., Terribile, L.C., 2017. Evaluating the effectiveness of Brazilian protected areas under climate change: a case study of *Micrurus brasiliensis* (Serpentes: Elapidae). Trop Conserv Sci 10, 1–8.
Chase, M.J., Schlossberg, S., Griffin, C.R., Bouché, P.J.C., Djene, S.W., Elkan, P.W., Ferreira, S., Grossman, F., Kohi, E.M., Landen, K., Omondi, P., Peltier, A., Selier, S.A.J., Sutcliffe, R., 2016. Continent-wide survey reveals massive decline in African savannah elephants. PeerJ 4, e2354.
Cushman, S.A., Chase, M., Griffin, C., 2010. Mapping landscape resistance to identify corridors and barriers for elephant movement in Southern Africa. In: Cushman, S.A., Huettmann, F. (Eds.), Spatial Complexity, Informatics and Wildlife Conservation. Springer.
Epps, C.W., Mutayoba, B.M., Gwin, L., Brashares, J.S., 2011. An empirical evaluation of the African elephant as a focal species for conservation planning in East Africa. Divers Distrib 17, 603–612.
Epps, C.W., Wasser, S.K., Keim, J.L., Mutayoba, B.M., Brashares, J.S., 2013. Quantifying past and present connectivity illuminates a rapidly changing landscape for the African elephant. Mol Ecol 22, 1574–1588.
Estes, R.D., 1991. The Behavior Guide to African Mammals. University of California Press, California.
Estes, J.G., Othman, N., Ismail, S., Ancrenaz, M., Goossens, B., Ambu, L.N., Estes, A.B., Palmiotto, P.A., 2012. Quantity and configuration of available elephant habitat and related conservation concerns in the lower Kinabatangan floodplain of Sabah, Malaysia. PLoS ONE 7 (10), e44601.
Estrada, E., Bodin, Ö., 2008. Using network centrality measures to manage landscape connectivity. Ecol Appl 18, 1810–1825.
Fan, D., Sun, Z., Li, B., Kou, Y., Hodel, R.G.J., Jin, Z., Zhang, Z., 2017. Dispersal corridors for plant species in the Poyang Lake Basin of southeast China identified by integration of phylogeographic and geospatial data. Ecol Evol 7, 5140–5148.
Franklin, J., 2010. Mapping Species Distributions: Spatial Inference and Prediction. San Diego State University, San Diego.
Garcia, R.A., Cabeza, M., Rahbek, C., Araújo, M.B., 2014. Multiple dimensions of climate change and their implications for biodiversity. Science 344, 1247579.
Gonzalez, P., Nielson, R.P., Lenihan, J.M., Drapek, R.J., 2010. Global patterns in the

vulnerability of ecosystems to vegetation shifts due to climate change. Glob. Ecol. Biogeogr. 19, 755–768.
Graham, M.D., Douglas-Hamilton, I., Adams, W.M., Lee, P.C., 2009. The movement of African elephants in a human-dominated land-use mosaic. Anim Conserv 12, 445–455.
Grainger, M., van Aarde, R.J., Whyte, I., 2005. Landscape heterogeneity and the use of space by elephants in the Kruger National Park, South Africa. Afr. J. Ecol. 43, 369–375.
Guan, B., Chen, W., Gong, X., Wu, T., Cai, Q., Liu, Y., Ge, G., 2016. Landscape connectivity of *Cercidiphyllum japonicum*, an endangered species and its implications for conservation. Eco Inform 33, 51–56.
Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25, 1965–1978.
Hijmans, R.J., Phillips, S., Leathwick, J., Elith, J., 2017. dismo: species distribution modeling. R package version 1.1-4. [URL]: https://CRAN.R-project.org/package=dismo.
Hoare, R.E., 1999. Determinants of human-elephant conflict in a land-use mosaic. J. Appl. Ecol. 35 (5), 689–700.
Hoare, R., 2000. African elephants and humans in conflict: the outlook for co-existence. Oryx 34, 34–38.
Hoglund, J., 2009. Evolutionary Conservation Genetics. Oxford University Press, Oxford.
Janžekovič, F., Novak, Tone, 2012. PCA – a powerful method for analyze ecological niches. In: Sanguansat, P. (Ed.), Principal Component Analysis - Multidisciplinary Applications. InTech, Croatia.
Johnson, C.N., Balmford, A., Brook, B.W., Buettel, J.C., Galetti, M., Guangchun, L., Wilmshurst, J.M., 2017. Biodiversity losses and conservation responses in the Anthropocene. Science 356, 270–275 (80-.).
Keeley, A.T.H., Beier, P., Keeley, B.W., Fagan, M.E., 2017. Habitat suitability is a poor proxy for landscape connectivity during dispersal and mating movements. Landsc Urban Plan 161, 90–102.
Kröpelin, S., Verschuren, D., Lézine, A.-M., Eggermont, H., Cocquyt, C., Francus, P., Cazet, J.-P., Fagot, M., Rumes, B., Russell, J.M., Darius, F., Conley, D.J., Schuster, M., von Suchodoletz, H., Engstrom, D.R., 2008. Climate-driven ecosystem succession in the Sahara: the past 6000 years. Science 320, 765–768 (80-.).
Lima-Ribeiro, M.S., Moreno, A.K.M., Terribile, L.C., Caten, C.T., Loyola, R., Rangel, T.F., Diniz-Filho, J.A.F., 2017. Fossil record improves biodiversity risk assessment under future climate change scenarios. Divers Distrib 23, 922–933.
Liu, Shiliang, Deng, Li, Dong, Shikui, Zhao, Qinghe, Yang, Juejie, Wang, Cong, 2014. Landscape connectivity dynamics based on network analysis in the Xishuangbanna Nature Reserve, China. Acta Oecol 55, 66–77.
Loyola, R.D., Lemes, P., Faleiro, F.V., Trindade-Filho, J., Machado, R.B., 2012. Severe loss of suitable climatic conditions for marsupial species in Brazil: challenges and opportunities for conservation. PLoS ONE 7, e46257.
Martínez-Freiría, F., Tarroso, P., Rebelo, H., Brito, J.C., 2016. Contemporary niche contraction affects climate change predictions for elephants and giraffes. Divers Distrib 22, 432–444.
Mazziotta, A., Triviño, M., Tikkanen, O.-P., Kouki, J., Strandman, H., Mönkkönen, M., 2015. Applying a framework for landscape planning under climate change for the conservation of biodiversity in the Finnish boreal forest. Glob Chang Biol 21, 637–651.
Mcrae, B.H., Dickson, B.G., Keitt, T.H., Shah, V.B., 2008. Using circuit theory to model connectivity in ecology, evolution and conservation. Ecology 89, 2712–2724.
de Oliveira, L.R., Loizaga De Castro, R., Cárdenas-Alayza, S., Bonatto, S.L., 2012. Conservation genetics of South American aquatic mammals: an overview of gene diversity, population structure, phylogeography, non-invasive methods and forensics. Mammal Rev 42, 275–303.
Pacifici, M., Foden, W.B., Visconti, P., Watson, J.E.M., Butchart, S.H.M., Kovacs, K.M., Scheffers, B.R., Hole, D.G., Martin, T.G., Akçakaya, H.R., Corlett, R.T., Huntley, B., Bickford, D., Carr, J.A., Hoffmann, A.A., Midgley, G.F., Pearce-Kelly, P., Pearson, R.G., Williams, S.E., Willis, S.G., Young, B., Rondinini, C., 2015. Assessing species vulnerability to climate change. Nat Clim Chang 5, 215–224.
Pereira, J., Saura, S., Jordán, F., 2017. Single-node vs. multi-node centrality in landscape graph analysis: key habitat patches and their protection for 20 bird species in NE Spain. Methods Ecol. Evol. 8, 1458–1467.
Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol Model 190, 231–259.
R Core Team, 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria [URL]: https://www.R-project.org/.
Rattis, L., Dobrovolski, R., Talebi, M., Loyola, R., 2018. Geographic range-scale assessment of species conservation status: a framework linking species and landscape features. Perspect Ecol Conserv. http://dx.doi.org/10.1016/j.pecon.2018.01.001.
Rubio, L., Bodin, Ö., Brotons, L., Saura, S., 2015. Connectivity conservation priorities for individual patches evaluated in the present landscape: how durable and effective are they in the long term? Ecography (Cop) 38, 782–791.
Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V., Woolmer, G., 2002. The human footprint and the last of the wild. Bioscience 52, 891.
Saupe, E.E., Qiao, H., Hendricks, J.R., Portell, R.W., Hunter, S.J., Soberón, J., Lieberman, B.S., 2015. Niche breadth and geographic range size as determinants of species survival on geological time scales. Glob Ecol Biogeogr 24, 1159–1169.
Saura, S., Pascual-Hortal, L., 2007. A new habitat availability index to integrate connectivity in landscape conservation planning: comparison with existing indices and application to a case study. Landsc Urban Plan 83, 91–103.
Saura, S., Rubio, L., 2010. A common currency for the different ways in which patches and links can contribute to habitat availability and connectivity in the landscape. Ecography (Cop) 33, 523–537.
Saura, S., Torné, J., 2009. Conefor Sensinode 2.2: a software package for quantifying the importance of habitat patches for landscape connectivity. Environ Model Softw 24, 135–139.
Saura, S., Estreguil, C., Mouton, C., Rodriguez-Freire, M., 2011. Network analysis to assess landscape connectivity trends: application to European forests (1990–2000). Ecol Indic 11, 407–416.
Sobek-Swant, S., Kluza, D.A., Cuddington, K., Lyons, D.B., 2012. Potential distribution of emerald ash borer: what can we learn from ecological niche models using Maxent and GARP? For Ecol Manag 281, 23–31.
Sukumar, R., 1991. The management of large mammals in relation to male strategies and conflict with people. Biol. Conserv. 55 (1), 93–102.
Summers, D.M., Bryan, B.A., Crossman, N.D., Meyer, W.S., 2012. Species vulnerability to climate change: impacts on spatial conservation priorities and species representation. Glob Chang Biol 18, 2335–2348.
Thouless, C.R., Dublin, H.T., Blanc, J.J., Skinner, D.P., Daniel, T.E., Taylor, R.D., Maisels, F., Frederick, H.L., Bouche, P., 2016. African Elephant Status Report 2016: An Update From the African Elephant Database. IUCN, Gland, Switzerland.
Thuiller, W., Georges, D., Engler, R., Breiner, F., 2016. biomod2: ensemble platform for species distribution modeling. R package version 3.3-7. [URL]: https://CRAN.R-project.org/package=biomod2.
Vanleeuwé, H., Gautier-Hion, A., 2002. Forest elephant paths and movements at the Odzala National Park, Congo: the role of clearings and Marantaceae forests. Afr J Ecol 36 (2), 174–182.
van Vuuren, D.P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, G.C., Kram, T., Krey, V., Lamarque, J.-F., Masui, T., Meinshausen, M., Nakicenovic, N., Smith, S.J., Rose, S.K., 2011. The representative concentration pathways: an overview. Clim Chang 109, 5–31.
Wan, H., Rasch, P.J., Zhang, K., Qian, Y., Yan, H., Zhao, C., 2014. Short ensembles: an efficient method for discerning climate-relevant sensitivities in atmospheric general circulation models. Geosci Model Dev 7, 1961–1977.
Wasser, S.K., Brown, L., Mailand, C., Mondol, S., Clark, W., Laurie, C., Weir, B.S., 2015. Genetic assignment of large seizures of elephant ivory reveals Africa's major poaching hotspots. Science 349, 84–87 (80-.).
Xun, D.Y., Liu, Y., 2014. Habitat connectivity analysis for conservation implications in an urban area. Acta Ecol Sin 34, 44–52.
Yan, Z., Petit-Maire, N., 1994. The last 140 ka in the Afro-Asian arid/semi-arid transitional zone. Palaeogeogr Palaeoclimatol Palaeoecol 110, 217–233.
Yannic, G., Pellissier, L., Ortego, J., Lecomte, N., Couturier, S., Cuyler, C., Dussault, C., Hundertmark, K.J., Irvine, R.J., Jenkins, D.A., Kolpashikov, L., Mager, K., Musiani, M., Parker, K.L., Røed, K.H., Sipko, T., Þórisson, S.G., Weckworth, B.V., Guisan, A., Bernatchez, L., Côté, S.D., 2013. Genetic diversity in caribou linked to past and future climate change. Nat Clim Chang 4, 132–137.
Zwiener, V.P., Padial, A.A., Marques, M.C.M., Faleiro, F.V., Loyola, R., Peterson, A.T., 2017. Planning for conservation and restoration under climate and land use change in the Brazilian Atlantic Forest. Divers Distrib 23, 955–966.